A VEGETATION ANALYSIS OF THE GREAT SMOKY MOUNTAINS

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I. Introduction

The vegetation of the Southern Appalachians has a central historical and geographic relation to the forests of eastern America, and many of the problems of those forests can best be studied there. The mountains are of great antiquity; and of the two major ranges, the Blue Ridge and Unakas, the younger Unakas have probably supported forests since the early Tertiary, when vegetation ancestral to that now in the area may have grown on the upper slopes. At all times the high relief of the ranges has caused high precipitation compared to the surrounding lowlands and has offered a variety of sites for the occupation of plants of widely different climatic adaptations. Much of the diverse vegetational mantle which the mountains supported has been preserved with little disturbance in the Great Smoky Mountains National Park, on the largest and highest segment of the Unaka Range. In the Smokies the great age, physiographic maturity, and subdued form have permitted the development of an almost continuous cover of forest. The soils of the Smokies are almost uniformly on the acid side, having been developed from noncalcareous metamorphic rocks of Cambrian age. The complex vegetational mantle of the Great Smoky Mountains was analyzed as a study of the structure and patterning of natural communities.

II. Methods

Methods of gradient analysis along the major environmental gradients of the range, those of elevation and of topographic site and moisture-balance, were used for the main part of the study. Six field transects along the topographic gradient of exposure and moisture-balance were made, each extending from a valley with mesic forests out onto the adjoining ridge supporting xeric exposed pine stands. Three hundred site counts, small vegetation samples from restricted and uniform sites, were taken at random locations, without regard to type. Each site count recorded a stand count of trees, usually 50 to 200 stems from the one-inch class up listed by estimated inches of diameter, notes on and lists of the undergrowth species and coverage, and a description of the site which included elevation, orientation and degree of slope, and topographic relation to valleys, slopes, and ridges. The site counts were arranged in composite transects, using stations containing several similar site counts at intervals along the major gradients of elevation and topographic ex-

posure. The site counts were used in composite stand counts in which several site counts were added together, and the composite counts were used to describe vegetation types. Quadrat studies and special stand counts were made in sixteen vegetation types for purposes of description. The site counts also were arranged in a mosaic chart, with the location of each spotted against an ordinate of elevation and an abscissa of topographic site, in order to study the distribution and patterning of types along these major gradients.

III. Gradient Analysis

Three composite transects of topographic site and moisture-balance in different elevation belts (1500-2500, 2500-3500, and 3500-4500 feet) were used to study the Eastern Forest System of deciduous trees, hemlock, and pines in the Smokies below 4500 feet. In each transect the site counts were arranged in stations according to their moisture-balances as indicated by the vegetation itself according to proportions of classes of trees (mesic, submesic, subxeric, and xeric) derived from the field transects. Along the gradient eastern forests show in sequence and without discontinuity forest types dominated by these classes: (1), cove forest mesophytics with broadleaf and, toward higher elevations, hemlock stands; (2), submesic red oak-pignut hickory forests, at lower elevations only; (3), subxeric chestnut oak-chestnut forest and heath stands; and (4), xeric pine forests and heaths. Along the gradient through these types there is a progressive decrease in tree stature and opening of the canopy toward xeric sites. As the canopy opens the shrub layer increases in cover and shifts in composition from non-ericaceous to preponderantly ericaceous and finally vacciniaceous. With increased shrub cover the herbs decrease toward xeric sites (the two strata show a rough inverse relation, with total coverage for both usually between 50 and 100 percent); and the herb layer changes from a high coverage of ferns and delicate umbrella-shaped herbs of rich mesic soils, to a sparse growth of tougher plants with leafy-stemmed and rosette forms prevailing in oak forests, and finally to the heterogeneous xeric group of the pine heaths, with grasses, austral composites and legumes, bracken fern, and ground heaths.

In the elevation transects of the eastern forests the site counts were arranged in stations at 200 or 300 foot intervals; and each of the four transects made contained only those site counts in which one of the four tree classes mentioned was most numerous. The transects thus compared vegetations of similar moisture-balance, though often of different topography of site, at different elevations. Differences with elevation are less

marked than differences with site in the eastern forests, but some significant changes occur. In the mesic transect a distinct zone dominated by subalpine beech appears above 4500 feet in gaps or saddles and the south-facing slopes leading down from them into valleys. In the submesic and subxeric transects northern red oak and white oak become dominant above 3700 feet in place of chestnut oak, which is dominant at lower elevations. In the xeric transect Virgina pine is most frequently dominant at low elevations, pitch pine at middle, and table mountain pine at high elevations. Like the pines, other species which are closely associated along the moisture gradient show themselves, when studied along the elevation gradient, to be fully independent in distribution. Moisture-balance appears, however, to be the more critically limiting gradient for many species in the eastern forests.

Elevation is the more critical gradient for the dominant trees of the boreal forests, with red spruce dominant from 4500 feet up through the lower part of the forests, Fraser fir dominant above 6000 feet. Boreal forest undergrowth was studied by topographic transects arranged in five steps — valleys, north slopes, intermediate slopes, south slopes, and ridges — and by exposure squares giving undergrowth coverages for different orientations of slope. Undergrowth shows, in contrast to the trees, minor differences with elevation but striking ones along the moisture gradient: from mesic herbs and shrubs identical with those of the mesic eastern forests in valleys, through a complex undergrowth of five strata — moss, oxalis, fern, Hugeria, and Viburnum — on north slopes, with all members decreasing into intermediate and south slopes, to dense Rhododendron heath on ridges. The red spruce-Fraser fir forests of the Southern Appalachians form a distinct geographic center in the Boreal Forest System with a high degree of endemism. They represent a distinctive member of the boreal forests, with status comparable to those of the western ranges.

In the Appalachians boreal forests reach their southern limit in the part of the Smokies where peaks over 6000 feet exist because these peaks served as sanctuary during the xerothermic period when the forests were eliminated from lower ones. The lower peaks in the southwest half of the range bear deciduous forests which range above 4500 feet to near their summits. Five stages, based on site and composition, were recognized in a topographic transect of these high-elevation deciduous forests: (1), beech-mixed forests on sheltered north slopes and north sides of gaps, (2), beech forests on south sides of gaps, (3), red oak-chestnut forests on open southerly slopes, (4), white oak-chestnut forests on some exposed south and southwest slopes, and (5), grassy balds on exposed summits.

IV. Theoretical Discussion

Study of the distributions of individual species along gradients shows they have the binomial or normal form and indicates that each species is distributed independently of others according to its own environmental tolerance and competitive ability. Distributions of the trees of the Smokies were plotted on charts against the gradients of elevation and site. All distributions appeared to form binomial figures, and no two distributions were alike. Each species along each of the many gradients, including competition, appears to behave as a law unto itself. Canopy dominants modify the environment in which undergrowth species are distributed, but undergrowth species respond, not to dominant species, but to environmental gradients determined partly by the dominants; and each undergrowth species responds to these gradients individualistically, according to its own physiology. Association of undergrowth and canopy species is a distributional coincidence of the physiologies of different plants responding to different, though not unrelated, gradients. The individualistic hypothesis of Gleason should be tested, and probably should be accepted with its implications.

Associations in synecology should be regarded as coincidental overlaps of specific distributions and should be approached through the distributions of the species involved. One of the most useful means of approaching reality in synecology is gradient analysis, the study of effective environmental gradients and the distributions of species, in terms of population or abundance, relative to those gradients. Since associations are consequences of specific distributions, they cannot be well understood except in terms of the distributions of species. Preliminary description of associations is often a useful and expedient method; but for careful vegetation analysis it is an essentially inverted scientific procedure. Ecological analysis should proceed from the primary phenomena, the distributions of species, to secondary phenomena, the associations resulting. Phytosociological constants for associations often have little meaning except as position relative to gradients is defined.

Much of the theory of synecology should be reconsidered from relative and individualistic viewpoints; and a different meaning should be sought for the association. Extreme limits, or other means of outlining distributions, are often useful for studying the occurrence of species together. For synecology, however, the mode, the point where a species reaches its maximum abundance, often in its environmental optimum, is usually the most useful single datum from distributions for community analysis. Since communities are determined by distributional coincidence or overlap, it is the close approximation of modes of different species

which produces the associations seen in nature. Species with their modes in the same area may be described as commodal; and a grouping of species from any structural part of a community which has modes together may be called a commodium, the basic unit above the level of the species and sample suggested for individualistic synecology. An association is an important commodium of dominants. Association of undergrowth commodia with those of dominants should not be assumed; herb and shrub commodia in the Smokies were found to have centers with the tree commodia in some cases, but to be independent of or actually intermediate to tree commodia in others.

The classes of trees, mesic to xeric, which were mentioned, are considered to be arbitrary groupings of species. In each case a few major species with modes close together, but separate, are used as the basis of a class; and minor species are grouped in with them. Because of the independence of distributions, the scattering of the modes of many species along the gradients, and the tapering form of binomial gradients, vegetations with related growth-forms may be continuous systems without discontinuity from one extreme to the other. Two such gradient systems were observed in the Smokies: the lower-elevation Eastern Forest System varying continuously with site from mesic cove forests through intermediate oak types to the xeric pine forests, and the higher-elevation Boreal Forest System of spruce and fir with a continuous series of undergrowth site types under similar canopies. A climax system is a broad geographic grouping of dominant species related by overlapping distributions, some degree of common history, and usually, outside extreme sites, by similar growth-forms.

The climax vegetations of an area are a broader or narrower section from the continuous and complex gradient system. They may be thought of as a single mantle of climax vegetation; but the diversity of this mantle, not its relation to a supposed climatic climax should be emphasized. Since climate can act only through a variety of sites usually supporting a variety of vegetations, the climatic climax is a concept rather remote from reality. The vegetation of an area can better be thought of as a diverse part of a gradient system. Within the system, however, associations or commodia of dominants with geographic centers may be recognized; and such an association may, when it occupies a fairly high proportion of available sites in an area, be regarded as the prevailing regional climax. Centers and prevailing climaxes can be judged only by relative standards. Associations are seldom important in one area and absent from an adjacent one; they occur in both but may occupy a greater proportion of the available sites in one area than in the other.

Ecotonal commodia between systems and between other communities of different growth-form are a widespread natural phenomenon. Ecotones observed in the Smokies were linked with one another by genera and species which they shared, and tended to be linked also with seral communities and with species occurring in the gradual transitions between associations. The species of ecotonal commodia are for the most part shrubs and small trees which increase in importance in the changed competitive conditions where other groups of plants overlap.

Distribution of the modes of species might, ideally, be almost at random within a system, but geography and history cause appearance of geographic centers like those of the eastern forests. Communities of extreme sites, either boreal or xeric, may form zones, with one or two dominants prevailing over each of the segments of the gradients, and with ecotones between the zones if they are dominated by different growth-forms. Because of the independence of species, split and complex distributions, and other complications, commodia have mostly a very low degree of reality and unity: and subjectivity is not eliminated from synecology by their use. They have, however, the virtue of realism, being based on observed distributions rather than on assumed associations.

V. Vegetation Types of the Smokies

On the basis of commodia of dominants Smoky Mountain vegetation is divided into types. The two independent systems in the range — the Boreal Forest System and Eastern Forest System — are the basis of the primary division into types; within systems the vegetation is subdivided according to commodia, physiognomy, and segregation of dominant species over some range of elevation and moisture-balance. Tree growth-forms are divided into abietines, dominating boreal forests and hemlock forests, deciduous mesic trees, dominating the cove forests, oaks, dominating with their associates intermediate types of eastern forests, and pines, dominating xeric eastern forests. Combinations with ericaceous shrubs are recognized — oak heath and pine heath —, as well as the reduced heath bald and grassy bald types.

Fifteen types considered topographic climaxes are distinguished and described:

I. Eastern Forest System

A. Mesic, non-quercine forests

1. Cove hardwood forest
2. Eastern hemlock forest
3. Subalpine beech forests

B. Intermediate, oak forests
   4. Red oak-pignut hickory forest
   5. Chestnut oak-chestnut forests
   6. Chestnut oak-chestnut heath
   7. Red oak-chestnut forest
   8. White oak-chestnut forest

C. Xeric, pine forests
   9. Virginia pine forests
   10. Pitch pine heath
   11. Table mountain pine heath

D. Extreme exposure type
   12. Grassy bald

II. Boreal Forest System

A. Boreal Forests
   13. Red spruce forest
   14. Fraser fir forest

B. Extreme exposure type
   15. Heath bald

Study of the distribution of these types in relation to elevation and topography on the mosaic chart shows how each fits into the continuous mantle of vegetation according to the distributions of its dominant species.

VITA

Robert Harding Whittaker was born in Wichita, Kansas, December 27, 1920, and attended school through college in Kansas, obtaining his A.B. *magna cum laude* from Washburn Municipal University, Topeka, in 1942. He spent three and one-half years in the Army Air Force Weather Service during the war, was trained in meteorology at Chanute Field, Rantoul, Illinois, in 1942, and served as a forecaster and weather station chief. After his discharge he entered the University of Illinois, in March, 1946, and has been attending continuously and working toward his Ph.D. in zoology since, except for two summers, one spent at Hopkins Marine Biological Station of Stanford University, Pacific Grove, California, the other spent in field work in the Great Smoky Mountains of Tennessee. He is a member of Phi Sigma and Sigma XI.